Journal of Comparative Psychology
2011, Vol. 125, No. 4, 436–445

0735-7036/11/$12.00 DOI: 10.1037/a0024516

The Limits of Endowment Effects in Great Apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*)

Patricia Kanngiesser
University of Bristol

Laurie R. Santos
Yale University

Bruce M. Hood
University of Bristol

Josep Call
Max Planck Institute for Evolutionary Anthropology

The endowment effect describes the bias that people often value things that they possess more than things they do not possess. Thus, they are often reluctant to trade items in their possession for items of equivalent value. Some nonhuman primates appear to share this bias with humans, but it remains an open question whether they show endowment effects to the same extent as humans do. We investigated endowment effects in all four great ape species (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*) by varying whether apes were endowed with food items (Experiment 1, $N = 22$) or tools that were instrumental in retrieving food (Experiment 2, $N = 23$). We first assessed apes' preferences for items of a pair and their willingness to trade items in their possession. We then endowed apes with one item of a pair and offered them to trade for the other item. Apes showed endowment effects for food, but not for tools. In Experiment 3, we endowed bonobos ($N = 4$) and orangutans ($N = 5$) with either one or 12 food items. Endowment effects did not differ between species and were not influenced by the number of endowed food items. Our findings suggest that endowment effects in great apes are restricted to immediate food gratification and remain unaffected by the quantity of food rewards. However, endowment effects do not seem to extend to other, nonconsumable possessions even when they are instrumental in retrieving food. In general, apes do not show endowment effects across a range of different commodities as humans typically do.

Keywords: endowment effect, biases, decision making, nonhuman primates, possession

Humans often show inconsistent preferences when faced with economic decisions. The endowment effect describes the bias to value things that one possesses more than things one does not possess (Thaler, 1980; Kahneman, Knetsch, & Thaler, 1990). For example, people usually demand more money for selling a good than they would be willing to pay for acquiring the same good. Similarly, when people are endowed with one good from a pair of goods and offered to trade for the other good, they regularly refuse to trade. This bias to overvalue things in one's possession has been ascribed to peoples' general tendencies to be averse to losses (Kahneman, Knetsch, & Thaler, 1991) or to adhere to the status quo (Samuelson & Zeckhauser, 1988).

This article was published Online First July 18, 2011.

Patricia Kanngiesser and Bruce M. Hood, School of Experimental Psychology, University of Bristol; Laurie R. Santos, Department of Psychology, Yale University; Josep Call, Department of Comparative and Developmental Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzip, Germany.

We thank the animal keepers at the Wolfgang Köhler Primate Research Centre for their help in conducting the studies, Annie Brookman for reliability coding, and Nathalia Gjersoe and Jan K. Woike for helpful feedback on earlier versions of the manuscript.

Correspondence concerning this article should be addressed to Patricia Kanngiesser, School of Experimental Psychology, 12a Priory Road, Bristol, BS8 1TU, United Kingdom. E-mail: patricia.kanngiesser@bris.ac.uk

Recent research into the evolution of economic behavior suggests that humans and nonhuman primates may share some biases in decision-making like the endowment effect (Brosnan et al., 2007; Lakshminarayanan, Chen, & Santos, 2008). In addition, they also appear to share an aversion to losses (Chen, Lakshminarayanan, & Santos, 2006). Importantly, however, while the endowment effect in humans is evident across a wide range of commodities (e.g., coffee mugs and chocolate: Knetsch, 1989; time: Hoorens, Remmers, & van de Riet, 1999; basketball tickets: Carmon & Ariely, 2000; lottery tickets: Bar-Hillel & Neter, 1996) and seems to emerge in early childhood (Harbaugh, Krause, & Vesterlund, 2000), this effect has only been demonstrated to a very limited extent in nonhuman primates. Specifically, when capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*) were endowed with different food items and offered to trade for items of equal value, they preferred to keep the food in their possession (Brosnan et al., 2007; Lakshminarayanan et al., 2008). However, chimpanzees did not prefer to keep nonfood items (i.e., toys) they were endowed with (Brosnan et al., 2007), indicating that endowment effects in nonhuman primates may be limited to food endowment. It thus remains unclear whether endowment effects in nonhuman primates really compare to the commodity-general effects found in humans. To date, previous studies have inadequately explored the scope of endowment effects in nonhuman primates either because they endowed nonhuman primates only with food (e.g., Lakshminarayanan et al., 2008) or

because they used objects that were of very limited value to nonhuman primates (e.g., toys, Brosnan et al., 2007). In addition, studies on endowment effects in primates so far have focused their investigation on one primate species at the time (chimpanzees or capuchin monkeys), but did not explore these effects across different species.

Here we present the first study to investigate endowment effects in all four great ape species (bonobos [*Pan paniscus*], chimpanzees [*Pan troglodytes*], gorillas [*Gorilla gorilla*], and orangutans [P*ongo pygmaeus*]) comparing food and nonfood objects of instrumental value; that is, tools that were used to retrieve food. As the previously established absence of endowment effects for toys may have been due to chimpanzee's lack of interest in objects that are not associated with food rewards, we wanted to ensure that all endowment objects (i.e., food items and tools) resulted in obtaining a food reward. In principle, all four ape species have been observed to use tools for food retrieval either in the wild or in the laboratory, though their propensity for manufacturing and using tools varies (Tomasello & Call, 1997).

For our experiments we adapted the procedure of Brosnan and colleagues (2007). In the beginning, we established that apes would principally be willing to trade food and tools in their possession. Next, apes were given a choice between items of a pair (i.e., between two different food items or between two different tools) to determine which of the two items they preferred. We then endowed them with one item of the pair and tested their willingness to trade for the other item and vice versa. Similar to Brosnan et al. (2007), we also included trials where apes were offered to trade for an item that was identical to the one they had been endowed with. This was to test whether apes may have had a preference for interacting with the experimenter over a preference for keeping items in their possession. In Experiment 1 (food endowment), we endowed apes with two different, highly favored food items (a banana slice and a food pellet). In order to facilitate trading of the food items, consumption of food was delayed by placing all items in transparent plastic tubes. In Experiment 2 (tool endowment), we endowed apes with two different sticks that could be used to retrieve a food reward on a platform. Half of the apes were first tested in Experiment 1, and half were first tested in Experiment 2.

In Experiment 3, we investigated food endowment effects further. First, we wanted to explore whether endowment effects would be attenuated by the amount of food apes were endowed with. We hypothesized that apes would trade more frequently when they were endowed with multiple food items (e.g., 12 identical items). Second, this design also allowed us to compare food endowment effects in different great ape species with sufficient statistical power, which we could not have achieved using the procedure of Brosnan et al. (2007) due to the small sample sizes available to us. We decided to focus our investigation on bonobos and orangutans as they represent one of the most closely and the most distantly related ape species to humans, respectively (e.g., Enard & Pääbo, 2004). In Experiment 3, we thus endowed bonobos and orangutans with either 1 or 12 food items of the same kind (e.g., 12 grapes) and offered to trade them for 1 or 12 food items of a different kind (e.g., 12 dried plums).

Experiment 1

Method

Subjects. Twenty-two great apes (5 bonobos [*Pan paniscus*], 12 chimpanzees [*Pan troglodytes*], 2 gorillas [*Gorilla gorilla*], 3 orangutans [P*ongo pygmaeus*]) participated in this experiment (see Table 1 for details). Sixteen additional apes (5 orangutans, 2 gorillas, 9 chimpanzees) began the experiment, but were excluded because they either failed the initial trading controls (12 apes) or were unwilling to participate after a few days (4 apes). All apes were housed at the Wolfgang Köhler Primate Research Center in Leipzig, where they had access to sleeping rooms, and seminatural indoor and outdoor enclosures. They were fed a variety of fruits and vegetables, occasionally supplemented by meat, eggs, and yoghurt, and had ad libitum access to water. Subjects were neither food nor water deprived. Testing took place in sleeping or testing rooms between 9 a.m. and 1 p.m. Whenever possible, apes were tested on consecutive days. All apes had at least some previous experience with trading procedures. Half of the apes were first tested in Experiment 1, and half were first tested in Experiment 2 (see Table 1 for details).

Procedure. We used a slice of banana (approx. 2-cm long) and a food pellet (monkey chow) as food for the endowment test. Both food items were highly favored by the apes and regularly used as food rewards. All food was placed in transparent, flexible tubes (15-cm long × 2.5-cm wide) to delay its consumption (see Figure 1A).

Table 1
Overview of Individuals Participating in Experiments 1 to 3

Species	Name	Gender	Age	Order of Experiment
Bonobo	Joey	M	25	Exp 2, Exp 1, Exp 3
Bonobo	Kuno	M	11	Exp 2, Exp 1, Exp 3
Bonobo	Limbuko	M	12	Exp 1, Exp 3
Bonobo	Ulindi	F	14	Exp 1, Exp 3
Bonobo	Yasa	F	10	Exp 1, Exp 2
Chimpanzee	Alex	M	7	Exp 1, Exp 2
Chimpanzee	Alexandra	F	8	Exp 1, Exp 2
Chimpanzee	Annett	F	8	Exp 1
Chimpanzee	Fifi	F	14	Exp 2
Chimpanzee	Fraukje	F	31	Exp 1, Exp 2
Chimpanzee	Frodo	M	14	Exp 2, Exp 1
Chimpanzee	Gertruida	F	14	Exp 2
Chimpanzee	Jahaga	F	14	Exp 2, Exp 1
Chimpanzee	Lome	M	6	Exp 1
Chimpanzee	Natascha	F	27	Exp 2, Exp 1
Chimpanzee	Pia	F	8	Exp 1, Exp 2
Chimpanzee	Riet	F	30	Exp 2
Chimpanzee	Robert	M	32	Exp 1
Chimpanzee	Sandra	F	14	Exp 1, Exp 2
Chimpanzee	Tai	F	5	Exp 2
Chimpanzee	Svela	F	12	Exp 1
Chimpanzee	Unyoro	M	11	Exp 2
Gorilla	Bebe	F	29	Exp 1, Exp 2
Gorilla	Viringika	F	13	Exp 1, Exp 2
Orangutan	Bimbo	M	27	Exp 2, Exp 1
Orangutan	Dokana	F	19	Exp 2, Exp 3
Orangutan	Dunja	F	34	Exp 1, Exp 2, Exp 3
Orangutan	Kila	F	8	Exp 3
Orangutan	Padana	F	10	Exp 2, Exp 3
Orangutan	Pini	F	19	Exp 2, Exp 1, Exp 3

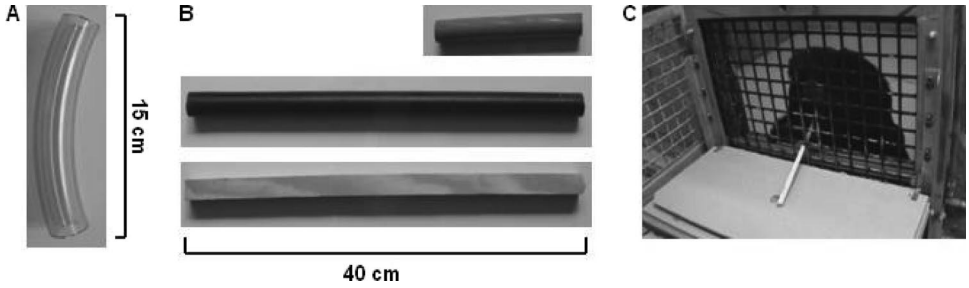

Figure 1. Endowment items used in Experiment 1 and 2. (A) shows a plastic tube used for the food endowment (15-cm long, 2.5-cm wide), (B) shows the different tools used for the tool endowment (40-cm long), and (C) shows a chimpanzee retrieving a grape in Experiment 2.

On day one, we gave apes one choice trial, where they could choose between a banana- and pellet-tube to assess which food they preferred. In the choice trial, apes were first shown both food tubes. Then, one food tube was placed on the left-hand side of a platform in front of the ape and the other tube was placed on the right-hand side of the same platform. We counterbalanced across apes whether the banana-tube was presented on the left-hand side or the right-hand side of the platform. Apes could indicate their choice by pointing to one of the food tubes. Only first points were scored and the respective food tube handed over to the ape. Next, apes participated in two trading-control trials where we tested whether they would be in principle willing to trade food items in their possession for the endowment food. Only apes that passed the trading-control trials participated in the subsequent endowment trials. We endowed apes with a piece of carrot in a plastic tube, as a piece of carrot is usually a less attractive food item for apes than a slice of banana or a pellet. In one of the trials, apes were offered to trade for a banana-tube and in the other trial they were offered to trade for a pellet-tube. The order of these trials was counterbalanced across apes. Each trade took place in the following way: we first showed the ape a banana-/pellet-tube and a carrot-tube. We then gave the carrot-tube to the ape. To elicit a trade we held the banana-/pellet-tube in one hand and started to gesture with the other, empty hand (that is, stretching out the hand and saying the ape's name and/or saying "Lass uns tauschen!" ["Let's trade!"]). However, trades only took place when the food in the tube that was in the apes' possession was left intact. If apes started to eat the food in the tubes, their behavior was scored as a nontrade. Apes that did not trade the carrot tubes for a banana- and a pellet-tube did not participate in the endowment trials to ensure that only those individuals participated that would be in principle willing to trade food items.

On days two to five, each ape experienced two endowment trials and two control trials with identical food items. We only conducted one trial per day and the order of trials was randomized across apes. In endowment trials, apes were endowed with a banana-tube and offered a trade for a pellet-tube (Trial 1) and vice versa (Trial 2). Trades occurred in the same manner as described above. In control trials, they were endowed with a banana-/pellet-tube and offered a trade for an identical banana-/pellet-tube (Trials 3 and 4). At the end of each endowment and control trial we asked apes to return the empty food tube, but did not offer a reward in return. This was to test whether apes were in principle willing to give up objects in their possession, particularly if these objects were of little value or use to them.

Finally, on day six, we repeated the two trading-control trials from day one by endowing apes with a carrot-tube and offering them a trade for a banana-/pellet-tube. This was done to retest apes' willingness to trade a piece of carrot for the more attractive food used in the endowment trials. We also gave apes four additional choice trials between banana- and pellet-tubes to assess the stability of their preferences across time.

Data scoring and analysis. Apes' choices and trading behaviors were coded live and from videotape by a single observer. A second independent observer coded a random sample of 20% of the data for reliability (interobserver agreement: $\kappa = .94$). Data was combined across species for all analyses, because the small number of animals did not yield to performing a statistical comparison with sufficient power. We analyzed the data using two-tailed McNemar change tests given the repeated measures design of the experiment. Means are reported with 95% confidence intervals.

Results

The majority of individuals from all four ape species chose a pellet over a banana slice (see Table 2 for details). However, when endowed with a banana slice, individuals of all four ape species—except orangutans—preferred to keep the banana-slice and did not trade it for a pellet. Similarly, when they were endowed with a pellet, individuals from all four species preferred to keep the pellet and refused to trade it for a banana slice. Combining the data from all four species, we compared the number of apes that chose a banana slice or a pellet in the choice trial to the number of apes that chose to keep the respective food item in the endowment trials. We found that 18% of apes chose a banana slice; however, when they were endowed with a banana slice and offered a trade for a pellet, significantly more apes (64%) preferred to keep the banana slice, $p = .006$ (see Figure 2A). Similarly, 82% of apes chose the pellet, but even more apes (95%) chose to keep the pellet when they were endowed with it, $p = .25$. In the control trials, where apes were offered a trade for an identical item, 86% of apes kept the banana slice and the pellet, respectively. When we compared the trading behavior of individuals in the control trials (i.e., whether individuals chose to keep or to trade the endowed food item for an identical one) to their trading behavior in the endowment trials, we found no significant difference—neither for banana slices, $p = .18$,

Table 2
Species' Preferences for Choosing or Keeping Items in Choice and Endowment Trials in Experiments 1 and 2

Experiment	Item	Species	*N*	% Chose in Choice Trial	% Kept in Endowment Trial
Exp 1	Banana Slice	Bonobos	5	20	60
Exp 1	Banana Slice	Chimpanzees	12	25	75
Exp 1	Banana Slice	Gorillas	2	0	100
Exp 1	Banana Slice	Orangutans	3	0	0
Exp 1	Pellet	Bonobos	5	80	100
Exp 1	Pellet	Chimpanzees	12	75	92
Exp 1	Pellet	Gorillas	2	100	100
Exp 1	Pellet	Orangutans	3	100	100
Exp 2	Plastic Tool	Bonobos	3	100	0
Exp 2	Plastic Tool	Chimpanzees	13	69	23
Exp 2	Plastic Tool	Gorillas	2	50	50
Exp 2	Plastic Tool	Orangutans	5	60	0
Exp 2	Wooden Tool	Bonobos	3	0	67
Exp 2	Wooden Tool	Chimpanzees	13	31	8
Exp 2	Wooden Tool	Gorillas	2	50	50
Exp 2	Wooden Tool	Orangutans	5	40	0

nor for pellets, $p = .50$. On an individual level, 59% of apes never traded any of the endowed food items in endowment trials, 36% of apes kept possession of their preferred item, 5% of apes (i.e., one ape) kept the nonpreferred item, and no apes traded both items (see Figure 2B).

Apes' food preferences remained very stable across time with 82% of apes choosing pellets at the beginning of the experiment and 82% of apes choosing pellets at the end of the experiment. Looking at individual preferences, only two apes (9%) reversed their food preferences at the end of the experiment, $p = .50$. One chimpanzee (Robert) switched from preferring pellets to preferring banana slices, while the reverse was true for one bonobo (Joey). All other apes either had the same preference as before or showed no preference (i.e., chose banana slices and pellets equally often in the four choice trials). Moreover, apes returned empty food tubes on average 96% (±5.6%) of the time after endowment and control trials without receiving any reward in return. While at the beginning of the experiment 100% of apes traded a piece of carrot for food that was used in the endowment trials, significantly fewer apes traded a piece of carrot for a banana slice (59%), $p = .004$, and for a pellet (64%), $p = .008$, respectively, after participation in the endowment and control trials.

Discussion

In Experiment 1, we found that apes were reluctant to trade banana slices and pellets once they had come to possess them. Qualitatively, this effect was present across all four ape species

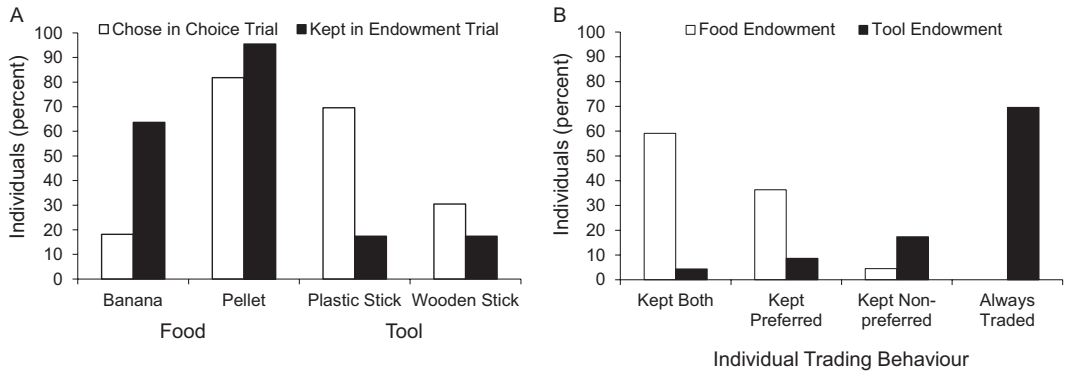

Figure 2. Results of Experiment 1 and 2 collapsed across all four species. (A) shows the comparison of choices in the choice trial and in the endowment trials. White bars indicate the percentage of individuals choosing the different food items and tools in the choice trials, black bars indicate the percentage of individuals choosing to keep the items in the endowment trials. (B) shows individuals' trading behavior in Experiments 1 and 2. White bars indicate trading behavior in the food endowment trials (Experiment 1) and black bars indicate trading behavior in the tool endowment trials (Experiment 2). "Kept Both" refers to individuals who kept items in both endowment trials and never traded; "Kept Preferred" refers to individuals who only kept the item they preferred as indicated by their choice in the choice trial; "Kept Nonpreferred" refers to individuals who kept the item they did not prefer; and "Always Traded" refers to individuals who always traded items.

with the exception of orangutans, who had a very strong preference for pellets and preferred to trade banana slices for pellets. While this effect was significant for banana slices across species, it was nonsignificant for pellets. However, since the majority of apes chose pellets in the choice trial, the difference between the choice and the endowment trials could not have reached significance even if all apes had kept their pellets. In fact, all apes but one kept pellets when offered to trade for banana slices. Furthermore, focusing on the individual level, more than half the apes never traded any of the food items they were endowed with. These findings indicate that endowment effects for food are prevalent across different great ape species on the level of the group as well as on the level of the individual. Although we did not find endowment effects in orangutans, this may have been due to methodological limitations and in particular the very small sample size. We return to this issue again later in Experiment 3, where we conducted a direct comparison of food endowment effects in orangutans and bonobos.

Control trials revealed that apes preferred to keep food in their possession even when offered to trade for identical food items. The fact that trading rates between endowment and control trials did not differ indicates that apes may have focused primarily on keeping highly valued food in their possession—irrespective of the alternative food they were offered. Moreover, at the end of the experiment, about 40% of the apes refused to trade pieces of carrot for endowment food. It is possible that some apes developed a general reluctance for trading food in their possession while participating in the endowment and control trials, which then may have carried-over to food items that they were initially willing to trade. Alternatively, some apes may have perceived trading of food as increasingly risky as time went by and thus preferred to keep food in their possession, disregarding the alternative food on offer. Their reluctance to trade food items in their possession, however, cannot be attributed to a general reluctance to hand over possessions: Apes traded pieces of carrot for endowment food at the beginning of the study and, in addition, regularly returned empty food tubes after endowment and control trials. This indicates that they were in principle prone to trading items in their possession.

To further investigate whether apes would show endowment effects across a range of different commodities, we conducted a second experiment, where we endowed apes with tools that were instrumental in retrieving food.

Experiment 2

Method

Subjects. Twenty-three apes (3 bonobos [*Pan paniscus*], 13 chimpanzees [*Pan troglodytes*], 2 gorillas [*Gorilla gorilla*], 5 orangutans [P*ongo pygmaeus*]) participated in Experiment 2 (see Table 1 for details). Thirteen additional apes (2 bonobos, 7 chimpanzees, 2 gorillas, 2 orangutans) began the experiment, but were excluded because they either failed the initial trading-control (6 apes), the familiarization trials (1 ape) or were unwilling to participate after a few days (6 apes). All apes were housed and tested at the Wolfgang Köhler Primate Research Center in Leipzig.

Procedure. In this experiment, apes had to use stick-like tools to get access to half a grape on a platform outside the testing room (see Figure 1C). We used two functional tools (a wooden stick and a black plastic stick, each 40-cm long), that were long enough to reach the grape-half on the platform (see Figure 1B). We also used one nonfunctional tool (a blue wooden stick, 15-cm long), that was too short to complete the task (see Figure 1B).

On day one, apes participated in familiarization trials, one choice trial, and two trading-control trials. Apes were familiarized with the task by presenting one of the functional tools, the nonfunctional tool, and half a grape on a platform for up to six times. One tool was placed on the left-hand side of the platform and the other tool on the right-hand side of a platform in front of the ape. We counterbalanced across apes whether the plastic tools was presented on the left-hand side or the right-hand side of the platform. Next, we placed half a grape in the middle of the platform at equidistance from the two tools. Apes could indicate their choice by pointing to one of the tools. Only the first pointing instance was scored and the respective tool was given to the ape. The ape could then use that tool to retrieve the half grape. As only one of the functional tools was presented per trial, the order of presenting the two tools was alternated for up to six trials. Apes only participated in the experiment if they chose the functional tool in two successive trials and retrieved the food successfully. After familiarization with the task, apes experienced one choice trial, where we gave them a choice between the two functional tools. In the choice trial, one functional tool was placed on the left-hand side of the platform and the other functional tool was placed on the right-hand side. Then, a grape was placed in the middle of the platform and apes could indicate which tool they wanted to use by pointing to the respective tool. The choice trial was conducted to assess which of the two functional tools they preferred. Finally, apes participated in two trading-control trials where we tested their willingness to trade the nonfunctional tool for a functional one. In one of the trials, apes were given the nonfunctional tool and offered a trade for the plastic tool. In the other trial, they were offered a trade of the nonfunctional tool for the wooden tool. The order of trading-control trials was counterbalanced across apes. Only apes that passed both trading-control trials participated in the study. Trades were similar to Experiment 1 with the following exceptions: Apes were first shown the two tools, then given the nonfunctional tool and offered a trade for the functional tool. However, apes had to trade tools within 15 seconds, during which no food was available on the platform. This delay was introduced because a pilot experiment had revealed that apes would not attend to the experimenter if food became available immediately. After 15 seconds—irrespective of whether apes had traded or not—a half grape was put on the platform.

On days two to five, each ape experienced two endowment trials and two control trials with identical tools. We only conducted one trial per day and the order of trials was randomized across apes. In endowment trials, apes were endowed with the wooden stick and offered a trade for the plastic stick (Trial 1) and vice versa (Trial 2). Trades occurred in the same manner as described above. In control trials, they were endowed with a wooden stick or a plastic stick and offered a trade for an identical wooden stick or plastic stick (Trial 3 and 4).

On day six, we repeated the two trading-control trials from day one by endowing apes with the nonfunctional tool and offering them a trade for the functional tools (one trial for each functional tool). This was done to retest apes' willingness to trades nonfunctional tools for the functional tools used in the endowment trials.

We also gave apes four additional choice trials between the two functional tools to assess the stability of their preferences across time.

Finally, on day seven, we conducted two further trading-control trials. However, this time we endowed apes with one of the functional tools and offered to trade for the nonfunctional tool (one trial for each functional tool). We introduced this final trading-control to assess whether apes would engage in trading of tools even if it did not result in securing a food reward.

Data scoring and analysis. Data scoring and analysis were identical to Experiment 1 (interobserver agreement: $\kappa = 1.0$). In addition, we compared apes' trading behavior in the endowment trials in Experiment 1 and 2 using Fisher's exact tests, given that not all individuals had participated in both experiments.

Results

Individuals from three ape species—with the exception of gorillas—had a tendency to choose the plastic tool over the wooden tool (see Table 2 for details). When endowed with the plastic tool, however, the majority of individuals traded the plastic tool for the wooden tool. Similarly, chimpanzees and orangutans (but less so bonobos and gorillas) preferred to trade the wooden tool for the plastic tool. Combining the data from all four species, we compared the number of apes that chose the plastic or the wooden tool in the choice trial to the number of apes that chose to keep the respective tools in the endowment trials. We found that 70% of apes chose the plastic tool (see Figure 2); however, when apes were endowed with the plastic tool and offered to trade for the wooden tool, significantly fewer apes (17%) kept the plastic tool, $p = .002$. Similarly, 30% of apes chose the wooden tool, but fewer apes (17%) kept the wooden when they were endowed with it, $p = .55$. In the control trials, where apes were offered to trade for an identical tool, 39% of apes kept the plastic tool and 22% of apes kept the wooden tool, respectively. Trading behavior in these control trials did not differ significantly from trading behavior in endowment trials—neither for the plastic tool, $p = .13$, nor for the wooden tool, $p > .99$. On an individual level, 4% of apes (i.e., one ape) never traded any of the endowed tools, 9% of apes kept possession of their preferred tool, 17% of apes kept the nonpreferred tool, and 70% of apes traded both items (see Figure 2B).

Apes' preferences remained stable across time with 70% of apes choosing the plastic tool before the endowment trials and 63% of apes choosing it at the end of the experiment. Looking at individual preferences, five apes (22%) reversed their tool preferences at the end of the experiment, $p = .06$. Three chimpanzees (Natascha, Pia, Unyoro) switched from preferring the plastic tool to preferring the wooden tool, while the reverse was true for one chimpanzee and one orangutan (Tai, Pini). The other apes either had the same preference as before or showed no preference (i.e., chose the plastic or the wooden tool equally often in the four choice trials). While at the beginning of the experiment 100% of apes traded the nonfunctional tool for functional tools, fewer apes traded the nonfunctional tool for the plastic tool (83%), $p = .13$, and for the wooden tool (87%), $p = .25$, after participation in the endowment and control trials. However, in the additional trading control trials, 68% of apes traded the plastic tool and 82% of apes traded the wooden tool for the nonfunctional tool.

Finally, we compared apes trading behavior in the endowment trials in Experiment 1 and Experiment 2. Apes traded endowed tools significantly more often than endowed food items, ps $< .002$.

Discussion

In Experiment 2, we found that apes preferred to trade tools in their possession, even though these tools could later be used to retrieve a food reward. Qualitatively, this effect was most pronounced in orangutans and chimpanzees. A comparison between apes' trading behavior in the current experiment and in Experiment 1 revealed that apes were more likely to trade tools than to trade food. Thus, in contrast to Experiment 1, apes did not show any endowment effects when they were endowed with tools. In fact, the majority of apes traded tools in both endowment trials, and most apes also traded endowed tools for identical ones in the control trials. Moreover, at the end of the experiment, the majority of apes even traded the functional tools for a nonfunctional tool, thereby forgoing the possibility to retrieve the food reward. Apes may thus have preferred trading tools with the experimenter to keeping those tools in their possession. Alternatively, they may have felt that they were supposed to hand over nonfood items to the experimenter. The overall finding, however, that apes were very willing to give up nonfood items—even if they were instrumental in accessing food—suggests that endowment effects in apes may be limited to food endowment.

In a third experiment we thus wanted to explore food endowment effects in apes further. We were particularly interested in investigating whether apes' trading behavior would be affected by the amount of food they were endowed with. We hypothesized that apes would be more willing to trade food if they had multiple items in their possession. In addition, we wanted to revisit the lack of endowment effects in orangutans observed in Experiment 1 and use a methodology that would allow us to draw direct comparisons between different great ape species with sufficient statistical power. We decided to compare orangutans to bonobos to be able to study whether endowment effects may be influenced by differences in phylogenetic relatedness to humans.

Experiment 3

Method

Subjects. Nine apes (4 bonobos [*Pan paniscus*], 5 orangutans [P*ongo pygmaeus*]) participated in Experiment 3, all of which had participated in the previous two experiments (see Table 1 for details). One additional bonobo was tested, but excluded because she had problems accessing the food in the tubes. All apes were housed and tested at the Wolfgang Köhler Primate Research Center in Leipzig.

Endowment food pre-test. Before conducting the endowment test, we tested apes' preferences for four different food items to determine two food items that would be preferred equally. We used half a peanut shell (containing one peanut), half a dried apricot, half a dried plum, and half a grape for the preference test. Individuals experienced two trials of forced choices between each pair of food items (six different pairs and 12 choices in total). The order of choices and the side of presentation (left or right) was counterbalanced. Bonobos chose dried apricots 25%, grapes 24%,

peanuts 28%, and dried plums 23% of the time. Orangutans chose dried apricots 11%, grapes 17%, peanuts 35%, and dried plums 20% of the time. We used grapes and dried plums as endowment foods, as they were best matched in terms of overall preferences across the two species.

Procedure. We used half a grape and half a dried plum as food for the endowment test. The tubes in which the endowment food was placed had a smaller diameter than in Experiment 1 (2 cm wide), so apes were provided with a stick to facilitate food retrieval from the tubes. The procedure was similar to the procedure in Experiment 1 with the following exceptions.

On the first day, apes were simultaneously given two carrot-tubes in a single trading-control trial. They were then offered a trade for one grape-tube and one plum-tube, which were offered in random order across apes. They experienced up to two trading-control trials a day on up to three consecutive days until they successfully passed one trial. After they had successfully passed one trading-control trial, apes experienced 12 choice trials between a grape- and a plum-tube to assess which food they preferred.

On days two to five, each ape experienced two 1-endowment trials where they were endowed with one food item and two 12-endowment trials where they were endowed with 12 food items of one kind. We only conducted one trial per day and the order of trials was randomized across apes. In 1-endowment trials, they were endowed with 1 grape-tube and allowed to trade for 1 plum-tube (Trial 1) and vice versa (Trial 2). In 12-endowment trials, they were endowed with 12 grape-tubes and allowed to trade for 12 plum-tubes (Trial 3) and vice versa (Trial 4). In each endowment trial—before apes were given access to the testing room—we first lined up the endowment tubes (i.e., the tubes apes were endowed with) in the apes' room. We then lined up the other tubes (i.e., the tubes that were offered for trade) on a platform exactly opposite the endowment tubes outside the testing room. The apes were then given access to the room. On day six, we repeated one trading-control trial from the first day by giving apes two carrot-tubes and offering a trade for one grape- and one plum-tube.

Data scoring and analysis. Data scoring and analysis were identical to Experiment 1 (interobserver agreement: $\kappa = .96$), with the exception that we used repeated measures ANOVA and *t* tests for analyzing our data to account for the fact that apes made multiple decisions in choice trials and 12-endowment trials. In order to score individual trading preferences in the 1-endowment and the 12-endowment trials, we defined keeping possession of items as keeping at least 10 out of 12 items in the 12-endowment trial (so that $p < .05$ according to a binomial-test against a chance value of .5). Means are reported with 95% confidence intervals.

Results

When given a choice between plums and grapes, preferences did not differ significantly between the two species, $t(7) = .48$, $p = .64$, $d = .34$ (see Figure 3). In addition, a repeated measures ANOVA with food type (plum vs. grape) and trial (1-endowment vs. 12-endowment) as within-subjects factors and species (bonobos vs. orangutans) as between-subjects factor revealed no significant effects of food type, $F_{1,7} = .80$, $p = .40$, $\eta_p^2 = .10$; of trial, $F_{1,7} = .02$, $p = .89$, $\eta_p^2 = .003$; and of species, $F_{1,7} = 1.24$, $p = .30$, $\eta_p^2 = .15$. As a consequence, the data were collapsed across species for all further analyses. Apes chose to keep grapes significantly more often in the 1-endowment trial ($M = 88.9 \pm 25.6\%$), $t(8) = 4.82$, $p = .001$, $d = -1.64$; and the 12-endowment trial ($M = 95.4 \pm 5.7\%$), $t(8) = 12.08$, $p < .001$, $d = -4.76$; than they choose grapes in the choice trials ($M = 20.4 \pm 15.1\%$). Similarly, apes chose plums significantly more often in the 1-endowment trial ($M = 100 \pm 0\%$), $t(8) = 3.12$, $p = .01$, $d = -1.04$; and the

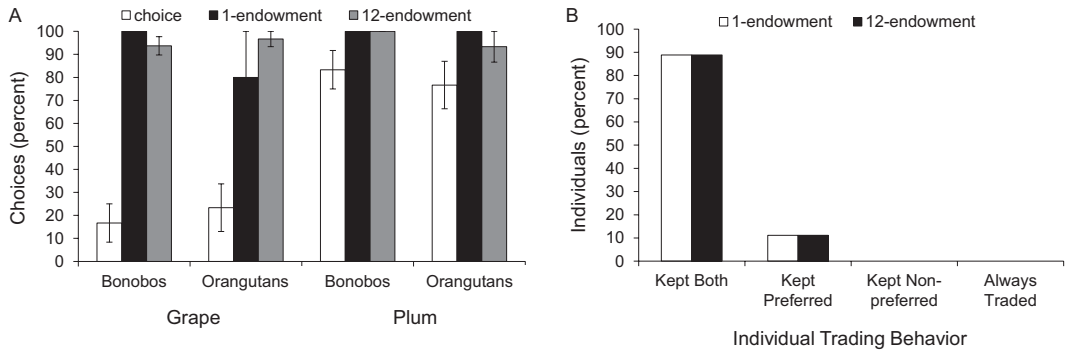

Figure 3. Results of Experiment 3. (A) shows average percentage of individuals' choices (with standard error) in the choice and endowment trials. White bars represent the average percentage of choices of the two food items in the choice trials, black bars represent the average percentage of choices to keep the endowed food item in the 1-endowment trials, and gray bars represent the average percentage of choices to keep the endowed food item in the 12-endowment trials. (B) shows individuals' trading behavior in Experiment 3. White bars indicate trading behavior in the 1-endowment trials and black bars indicate trading behavior in the 12-endowment trials. "Kept Both" refers to individuals who kept items in both endowment trials and never traded; "Kept Preferred" refers to individuals who only kept the item they preferred as indicated by their choice in the choice trial; "Kept Nonpreferred" refers to individuals who kept the item they did not prefer; and "Always Traded" refers to individuals who always traded items. In 12-endowment trials keeping of items was defined as keeping at least 10 out of 12 items, which indicates that individuals kept items significantly above chance (.5) according to a binomial-test.

12-endowment trial ($M = 96.3 \pm 8.5\%$), $t(8) = 3.62$, $p = .007$, $d = -1.47$; than they chose plums in the choice trials ($M = 79.6 \pm 15.1\%$). On an individual level, 89% of apes never traded any of the endowed food items, 11% of apes (i.e., 1 ape) kept possession of their preferred food items, and no apes kept the nonpreferred food items or traded both items (see Figure 3B). This was true for 1-endowment as well as 12-endowment trials.

Moreover, apes returned on average 84% ($\pm$ 10.9%) of empty tubes after endowment trials without receiving any reward in return. While at the beginning of the experiment 100% of apes traded a piece of carrot for food that was used in the endowment trials, fewer apes traded a piece of carrot for a grape (56%), $p = .13$, and for a plum (44%), $p = .06$, respectively, after participation in the endowment trials.

Discussion

In Experiment 3, orangutans and bonobos were reluctant to trade food in their possession independent of whether they were endowed with one or 12 identical food items. Moreover, we did not find any difference in endowment effects between bonobos and orangutans. This finding extends the results from Experiment 1 and indicates that endowment effects are present across all four great ape species. In addition, apes did not trade more frequently when endowed with more food items, indicating that the amount of endowed food (1 item vs. 12 items) did not have an influence on food endowment effects. Previously, a similar result was obtained for two groups of chimpanzees, where individuals were reluctant to trade food items in their possession for food of similar value after they had been endowed with 30 identical food items (Brosnan, Grady, Lambeth, Schapiro, & Beran, 2008). However, in addition to extending these findings to two other great ape species, namely bonobos and orangutans, we could also demonstrate that the number of endowed items did not play a significant role in influencing trading behavior.

Similarly to Experiment 1, apes returned empty food tubes on the majority of trials, indicating that reluctance to principally hand over items could not explain endowment effects for food. In addition, apes were again more reluctant to trade pieces of carrot for endowment food after participation in the endowment trials—though this effect was not significant, possibly due to the small number of individuals in this experiment. This decline in trading rates at the end of the experiment could indicate that for some apes endowment effects may have carried over to food that they were initially willing to trade with the experimenter. Alternatively, over time some apes may have perceived trades as increasingly risky and thus preferred to keep food in their possession irrespective of the food's value. However, previous studies investigating trading behavior in chimpanzees have found that chimpanzees can flexibly adapt their trading behavior depending on the value of the food involved in the exchanges (e.g., Lefebvre, 1982; Lefebvre & Hewitt, 1986). The decline in trading rates that we observed in our study thus remains puzzling, and further investigations into how great apes' trading behavior for food changes over time may be needed to shed more light on these findings.

General Discussion

In our study, apes from all four great ape species preferred to keep food in their possession once they were endowed with it. While previous studies have only demonstrated endowment effects for chimpanzees (Brosnan et al., 2007) and capuchin monkeys (Lakshminarayanan et al., 2008), our study showed that these effects extend to all four great ape species. In addition, we could demonstrate that food endowment is not affected by the number of food items apes were endowed with. These endowment effects could not be attributed to the apes being, in principle, reluctant to trade items, because apes reliably returned empty food tubes at the end of each trial without receiving a reward. However, apes did not show endowment effects for tools even though they were later used to retrieve food. In contrast to their performance in Experiments 1 and 3, apes tested in Experiment 2 frequently traded tools after being endowed with them. In fact, they traded tools more often than food, which indicates that apes treated the two commodities *food* and *tool* very differently.

In line with previous research, our findings suggest that endowment effects in all four great ape species (and other nonhuman primates) are genuinely limited to food endowment (Brosnan et al., 2007; Lakshminarayanan et al., 2008). The absence of an endowment effect for functional tools could be a result of the transitory nature of material possessions in nonhuman primates and the absence of any kind of (socially reinforced) ownership (Pryor, 2003). As a consequence, nonhuman primates may not value material possessions as humans typically do.

Alternatively, apes may have experienced trading tools as a low-cost and rewarding activity in itself. Throughout the study, apes were very prone to exchanging nonfood objects with human experimenters. For example, the majority of apes in Experiments 1 and 3 returned empty food tubes without receiving any reward in return. Apes were also very likely to trade tools for identical tools (while they showed the opposite behavior with regards to food). Furthermore, at the end of Experiment 2—despite having repeatedly experienced the contingencies of the set-up—the majority of apes traded functional tools for nonfunctional tools, thus forgoing the possibility of retrieving a food reward. Apes thus even paid short-term costs due to their disposition for trading nonfood objects. It is conceivable that apes valued exchange of nonfood items with the experimenter more than keeping those items in their possession.

Furthermore, differences between food and tool endowment could have been due to the presence or absence of food rewards. Even though tools were instrumental in retrieving food, no food was present during tool trades. Recent findings with human subjects suggest that the physical presence of a good influences people's valuation of that good. For example, people were willing to pay more for food when it was physically present than when they only read a description or saw an image of the food (Bushong, King, Camerer, & Rangel, 2010). Similarly, apes could have valued tools less than food because tools were only indicative of the presence of food. Under this view, the pattern of performance we observed—with apes showing an endowment effect for foods and not tools—may reflect differences in the salience of the reward across the two stimulus types.

Finally, food endowment effects in nonhuman primates may be caused by a different underlying process than endowment effects in humans. While endowment effects in humans are usually attributed to loss aversion (Kahneman et al., 1991), apes may simply find it difficult to inhibit the consumption of food in their possession. Past research has demonstrated that great apes can forgo

immediate rewards for future rewards under certain conditions: if they are offered a more preferred reward (chimpanzees: Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999), if food accumulates over time (chimpanzees and orangutans: Beran, 2002), if they are offered a larger piece of reward (chimpanzees: Dufour, Pelé, Sterck, & Thierry, 2007), or if they are offered a larger quantity of food (bonobos and chimpanzees: Rosati, Stevens, Hare, & Hauser, 2007). However, all of these studies have in common that the quantity (or the value) of the future food reward was higher than the value of the immediate reward. In contrast, it is inherent to endowment studies to use rewards that are very close in perceived value and quantity, which may constitute the crucial difference between tests of delay of gratification and tests of endowment effects. Indeed, Lakshminarayanan and colleagues (2008) found that capuchin monkeys showed no evidence of an endowment effect for food rewards when the food being offered was of higher quality (see Experiment 2). Likewise, apes in our study initially traded pieces of carrot for the more attractive endowment food and only stopped trading once both food items were similarly attractive (though for some individuals this effect carried over to trades at the end of the experiment where they were endowed with carrots and offered to trade for the endowment food). Future studies could investigate this issue further by substituting food items for tokens that represent the respective food. If apes were to show no endowment effects for tokens (i.e., when food is no longer directly present) than this would provide evidence that food endowment effects in apes may be driven by a lack of inhibition to consume possessed food. This lack of inhibition could also explain why we did not find endowment effects for tools, as food was not directly present during tool trades.

While humans show endowment effects across a wide range of different commodities (e.g., Knetsch, 1989; Carmon & Ariely, 2000), endowment effects in apes appear to be limited to endowment with food. This suggests that endowment effects in nonhuman primates may not really be comparable to the more generalized endowment effects found in humans. In addition, there is recent evidence that apes value the commodity food much more than humans (Rosati et al., 2007). Hence it is unclear whether humans would even show endowment effects for food determined for immediate consumption.

In our three experiments, we tested individuals from all four great ape species (bonobos, chimpanzees, gorillas, orangutans). Qualitatively, in Experiment 1, endowment effects seemed strongest in bonobos, chimpanzees and gorillas, whereas in Experiment 2 chimpanzees and orangutans were most prone to trading tools. Species differences were difficult to assess, however, due to the small number of individuals in all species apart from chimpanzees. Yet, in Experiment 3 we directly compared endowment effects for food in orangutans and bonobos, which represent humans' closest and most distant great ape relatives, respectively (e.g., Enard & Pääbo, 2004). We found no species difference, which indicates that endowment effects for food are present across the entire great ape lineage. In addition, evidence from studies with capuchin monkeys (Lakshminarayanan et al., 2008) suggests that these effects may even be shared with more distantly related primates. Even though recent studies on risk preferences have revealed that chimpanzees are more risk prone than bonobos (Heilbronner, Rosati, Stevens, & Hare, 2008), our study found no differences in endowment effects for food. One possible explanation for the different findings could be that trades in endowment situations are associated with less risk and thus may not tap into the same mechanisms responsible for creating divergent risk preferences in chimpanzees and bonobos for risky choices.

In conclusion, we replicated the endowment effect on food by chimpanzees and extended these findings to all other great ape species. However, we were unable to elicit endowment effects with objects instrumental in retrieving food. Our results therefore suggest that a spontaneous overvaluation of nonconsumable possessions may be a uniquely human quality not shared with other nonhuman primates.

References

Bar-Hillel, M., & Neter, E. (1996). Why are people reluctant to exchange lottery tickets? *Journal of Personality and Social Psychology, 70,* 17–27.

Beran, M. J. (2002). Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). *Journal of General Psychology, 129,* 49–66.

Beran, M. J., Savage-Rumbaugh, E. S., Pate, J. L., & Rumbaugh, D. M. (1999). Delay of gratification in chimpanzees (*Pan troglodytes*). *Developmental Psychobiology, 34,* 119–127.

Brosnan, S. F., Grady, M., Lambeth, S., Schapiro, S., & Beran, M. J. (2008). Chimpanzee autarky. *PLoS ONE, 3,* e1518.

Brosnan, S. F., Jones, O. D., Lambeth, S. P., Mareno, M. C., Richardson, A. S., & Schapiro, S. J. (2007). Endowment effects in chimpanzees. *Current Biology, 17,* 1704–1707.

Bushong, B., King, L. M., Camerer, C. F., & Rangel, A. (2010). Pavlovian processes in consumer choice: The physical presence of a good increases willingness-to-pay. *American Economic Review, 100,* 1556–1571.

Carmon, Z., & Ariely, D. (2000). Focusing on the forgone: How value can appear so different to buyers and sellers. *Journal of Consumer Research, 27,* 360–370.

Chen, M. K., Lakshminarayanan, V., & Santos, L. R. (2006). How basic are behavioral biases? Evidence from capuchin monkey trading behavior. *Journal of Political Economy, 114,* 517–537.

Dufour, V., Pelé, M., Sterck, E. H. M., & Thierry, B. (2007). Chimpanzee (*Pan troglodytes*) anticipation of food return: Coping with waiting time in an exchange task. *Journal of Comparative Psychology, 121,* 145–155.

Enard, W., & Pääbo, S. (2004). Comparative primate genomics. *Annual Review of Genomics and Human Genetics, 5,* 351–378.

Harbaugh, W. T., Krause, K., & Vesterlund, L. (2000). Are adults better behaved than children? Age, experience, and the endowment effect. *Economics Letters, 70,* 175–181.

Heilbronner, S. R., Rosati, A. G., Stevens, J. R., & Hare, B. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzee and bonobos. *Biology Letters, 4,* 246–249.

Hoorens, V., Remmers, N., & van de Riet, K. (1999). Time is an amazingly variable amount of money: Endowment and ownership effects in the subjective value of working time. *Journal of Economic Psychology, 20,* 383–405.

Kahneman, D., Knetsch, J. L., & Thaler, R. H. (1990). Experimental tests of the endowment effect and the coarse theorem. *Journal of Political Economy, 98,* 1325–1348.

Kahneman, D., Knetsch, J. L., & Thaler, R. H. (1991). The endowment effect, loss aversion and status quo bias. *Journal of Economic Perspectives, 5,* 193–206.

Knetsch, J. L. (1989). The endowment effect and evidence of nonreversible indifference curves. *The American Economic Review, 79,* 1277–1284.

Lakshminarayanan, V., Chen, K. M., & Santos, L. R. (2008). Endowment effect in capuchin Monkeys. *Philosophical Transactions of the Royal Society B, 363,* 3837–3844.

Lefebvre, L. (1982). Food exchange strategies in an infant chimpanzee. *Journal of Human Evolution, 11,* 195–204.

Lefebvre, L., & Hewitt, T. A. (1986). Food exchange in captive chimpanzees. In D. M. Taub & F. A. King (Eds.), *Current perspectives in primate social dynamics* (pp. 476–486). New York: Van Nostrand Reinhold.

Pryor, F. L. (2003). What does it mean to be human? A comparison of primate economies. *Journal of Bioeconomics, 5,* 97–146.

Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2007). The evolutionary origins of human patience: Temporal preferences in chimpanzees, bonobos, and human adults. *Current Biology, 17,* 1663–1668.

Samuelson, W., & Zeckhauser, R. (1988). Status quo bias in decision making. *Journal of Risk and Uncertainty, 1,* 7–59.

Thaler, R. H. (1980). Toward a positive theory of consumer choice. *Journal of Economic Behavior and Organization, 1,* 39–60.

Tomasello, M., & Call, J. (1997). *Primate cognition.* New York: Oxford University Press.

Received August 23, 2010
Revision received May 11, 2011
Accepted May 31, 2011 ■